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SEASONAL PATTERNS IN THE BIOCHEMICAL CONSTITUENTS AND BODY COMPONENT INDEXES OF THE MURICID GASTROPOD, *THAIS HAEMASTOMA*

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There are several methods currently employed in determining reproductive cycles in marine invertebrates. One of the most useful to date is that of determining body component/body weight ratios. These ratios, known collectively as body component indexes, allow for an overall view of the entire reproductive state of an organism and, coupled with determination of various biochemical constituents (*i.e.*, lipid, carbohydrate and protein), enable one to trace the accumulation and mobilization of organic reserves associated with annual reproductive cycles. Other methods of studying the reproductive states of marine invertebrates have been summarized by Giese (1959) and include spawning, numbers of larvae, appearance of ripe gametes, brooding of eggs and relative size of gonads.

The reproductive cycles of a variety of temperate species of prosobranch gastropods have been established. Houston (1971) utilized histological and histochemical techniques in studying the reproductive biology of two West Coast species, *Thais canaliculata* and *T. emarginata*. Seasonal cycles in *T. lamellosa* have been determined using the index method (Stickle, 1973; Lambert and Dehnel, 1974). Other prosobranchs which have been studied include *Fusitriton oregonensis* by Stickle and Mrozek (1973), *Haliotis cracherodii* by Webber (1970) and Webber and Giese (1969) and *Littorina littorea* by Williams (1970).

The capsule-albumin gland index has been determined to be the best component indicator of reproductive readiness in several species of prosobranchs, including *F. oregonensis* (Stickle and Mrozek, 1973) and *T. lamellosa* (Stickle, 1973). In a subtropical species such as *Thais haemastoma*, where spawning is intermittently interspersed with feeding, short term fluctuations in the body component indexes may be considerable.

Energy requirements during the reproductive period of an organism may be relatively expensive. For example, 30% of the prespawning soft body weight of *F. oregonensis* was lost during aggregation and capsule deposition (Stickle and Mrozek, 1973), while 34% was lost during the same period by *T. lamellosa* (Stickle, 1973). Many animals meet the metabolic expense of spawning by drawing on reserve materials accumulated during a prespawning refractory period. Seasonal changes in body component indexes have been shown to reflect fluctuations in biochemical constituents in several species of marine gastropods. Stickle (1975) found seasonal changes in the protein, carbohydrate and lipid content of body components in *T. lamellosa* to be due predominantly to changes in the component indexes and not to fluctuations in constituents levels. Bistransin (1976) found similar results in the subtropical *Littorina irrorata*.

These analyses were performed to determine seasonal patterns in the body component indexes and biochemical content and level of lipid, carbohydrate and protein in the subtropical prosobranch gastropod, *T. haemastoma*.

Materials and Methods

Body component indexes

Adult specimens (>30 mm) of *Thais haemastoma* were collected at approximately monthly intervals from September, 1973, through December, 1974. Animals were obtained from the concrete pilings supporting the bridge spanning Caminada Pass, Louisiana. Water temperature and salinity were determined at each collection. Live animals were transported to Louisiana State University where they were placed in collection jars or plastic containers and stored at −20° C. Dissections were begun in the fall of 1975 and continued through the spring of 1977.

Animals were removed from the freezer and encrustations scraped from the shell. Shell length, taken as the distance from the apex to the tip of the siphonal canal, was determined with a vernier caliper. The shell and foot were blotted dry and the entire animal including the shell and operculum was weighed. This weight was designated as the entire weight. When animals were completely thawed the shell was cracked and the operculum and all shell pieces removed. The animal was immediately dissected into body components and the total wet weight determined. The shell weight was taken as the entire weight minus the soft body wet weight. Male body components consisted of shell, body water, foot, testis-digestive gland (TDG), and remaining visceral mass (RVM). Female body components consisted of shell, body water, foot, ovary-digestive gland (ODG), remaining visceral mass (RVM) and capsule-albumin gland (CAG). Individual components were flash frozen between two cakes of dry ice, lyophilized to dryness and placed in a desiccator. Dried components were weighed to the nearest mg, and this weight was designated as the component dry weight. Lyophilized components were stored at −20° C. Individual body component indexes were calculated according to the method of Stickle (1973).

Biochemical analyses

Lyophilized body components were removed from the freezer and warmed to room temperature in a dessicator. Individual components were ground in a

Thomas-Wiley tissue grinder and stored at −20° C in one dram glass vials with cork stoppers. Protein and carbohydrate were extracted by refluxing 10 mg of ground tissue in 20% KOH at 100° C. The digest was diluted to yield a final KOH concentration of 1%. Aliquots of this dilution were used in all subsequent protein and carbohydrate analyses. Protein was determined using a modified Gornall biuret test (Gornall, Bardawill and David, 1949). Samples were corrected for turbidity and color interference by subtracting a specific minus copper reference tube from each tube reading. Bovine serum albumin was used as a reference standard. Total carbohydrate was determined by the method of Dubois, Gilles, Hamilton, Rebers and Smith (1956) using glycogen as a reference standard.

Lipids were extracted from dry, ground tissue using a methanol: chloroform: water (2: 1: 0.8) procedure (Bligh and Dyer, 1959; Kates, 1972). Total lipids were determined gravimetrically.

Biochemical level and content

Total protein, carbohydrate and lipid level data are presented as percentage of dry weight. Biochemical content (total present per component of a 100 g standard animal) was determined by the method of Stickle (1975) where content equals the decimal fraction of level times the component index.

Statistical analyses

All variables are presented as the mean plus or minus the confidence interval at the ninety-five per cent level of significance. One way analysis of variance (ANOVA) was used to determine the significance of variation in soft body indexes and in biochemical content and level on a seasonal basis. The CAG index and the RVM, ODG, TDG and CAG biochemical content and level of males and females were further studied using Duncan's Multiple Range Test. "Foot" data was not analyzed with the Duncan's Test because variations in that component are minor.

Shell weight–shell length ratios were analyzed using the maximum r^2 improvement procedure of the dependent variable. Shell indexes were regressed on the mean shell weight–shell length ratios to determine whether or not index variations were due to fluctuations in the shell or in the soft body components. Differences were termed significant if $P < 0.05$ and highly significant if $P < 0.01$. All statistical analyses except the 95% confidence intervals were programmed and performed using a statistical analyses system (Barr, Goodnight, Sall and Helwig, 1976).

Results

Body component indexes

The shell, body water and dry weight indexes and collection data for males and females are found in Table I. Shell weight/shell length ratios exhibited significant variations with time; however, linear regression analysis of monthly mean shell indexes on mean shell weight/shell length ratios over the course of the study indicates there was no significant relationship between these two variables in either sex. Body water and dry weight indexes cycled inversely to the shell index.

TABLE I

Collection data, shell, body water and dry weight indexes for male and female Thais haemastoma. *Indexes are presented as the mean plus and minus the ninety-five per cent confidence limit. N.D. indicates no data.*

Date	Water temp. (°C)	Salinity (‰)	Sample ♂	Size ♀	Shell index		Body water Index		Dry weight Index	
					♂	♀	♂	♀	♂	♀
Sept. 1973	30.5	18.0	14	9	77.35 ± 2.09	78.73 ± 2.87	16.64 ± 0.47	15.72 ± 2.17	6.01 ± 0.68	5.55 ± 0.80
Oct. 1973	25.2	22.0	11	5	73.79 ± 1.22	76.13 ± 2.81	19.60 ± 1.13	15.85 ± 1.78	6.59 ± 0.80	6.02 ± 1.82
Dec. 1973	13.8	27.0	5	8	80.64 ± 1.94	80.57 ± 3.30	13.00 ± 1.78	12.66 ± 2.13	6.36 ± 0.69	5.63 ± 0.76
Jan. 1974	10.0	19.0	13	9	78.00 ± 1.38	82.55 ± 2.74	15.58 ± 0.91	13.05 ± 1.63	6.55 ± 0.79	4.40 ± 1.07
Feb. 1974	20.0	12.0	13	9	83.79 ± 1.03	83.75 ± 1.18	12.25 ± 0.87	12.03 ± 0.94	3.98 ± 0.33	4.22 ± 0.40
March 1974	21.5	11.0	17	7	84.15 ± 1.23	84.00 ± 2.76	11.93 ± 0.08	12.03 ± 1.58	3.92 ± 0.49	3.53 ± 0.74
April 1974	24.9	16.0	12	12	76.33 ± 1.56	77.43 ± 1.62	17.32 ± 0.94	15.82 ± 0.96	6.36 ± 0.76	6.75 ± 0.73
May 1974	N.D.	N.D.	20	14	80.68 ± 1.15	81.95 ± 1.11	14.45 ± 0.75	13.18 ± 0.82	4.88 ± 0.45	4.87 ± 0.42
June 1974	29.0	23.5	24	9	82.21 ± 0.78	81.83 ± 1.98	13.20 ± 0.61	13.07 ± 1.32	4.58 ± 0.21	5.11 ± 0.73
July 1974	32.5	19.0	19	9	84.31 ± 1.41	83.31 ± 2.43	10.90 ± 0.90	11.34 ± 1.62	4.59 ± 0.51	4.88 ± 0.81
Aug. 1974	22.8	20.0	21	8	82.71 ± 1.62	83.71 ± 2.64	12.60 ± 1.11	11.28 ± 1.76	4.69 ± 0.57	5.00 ± 1.02
Sept. 1974	27.8	20.5	13	13	80.71 ± 2.16	80.80 ± 1.69	13.94 ± 1.34	13.92 ± 1.00	5.36 ± 0.93	5.28 ± 0.73
Oct. 1974	22.5	28.0	10	6	81.21 ± 1.55	84.67 ± 1.76	13.60 ± 1.13	11.01 ± 1.13	5.50 ± 0.78	3.99 ± 1.30
Nov. 1974	19.0	30.5	10	10	84.92 ± 1.83	85.98 ± 1.26	11.35 ± 1.15	10.72 ± 0.94	3.72 ± 0.84	3.30 ± 0.74
Dec. 1974	11.5	23.5	7	1	84.64 ± 1.73	85.49	11.31 ± 1.57	10.74	4.05 ± 0.24	3.77

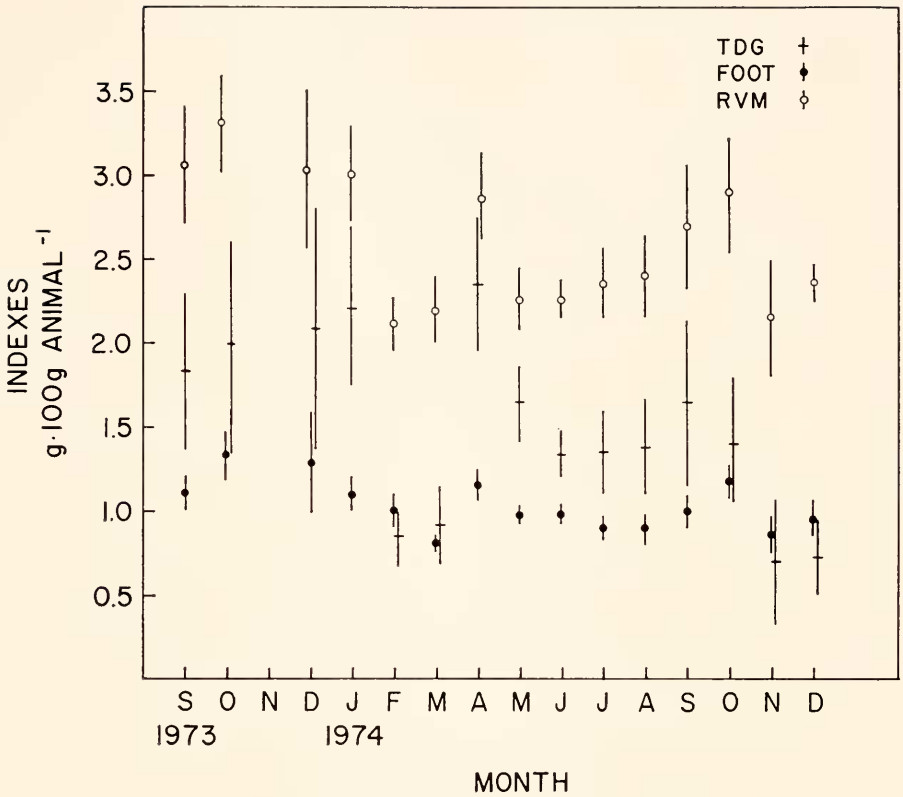

FIGURE 1. Body component indexes in *Thais haemastoma*. Male testis-digestive gland (TDG), remaining visceral mass (RVM) and "foot" indexes are presented as the mean (symbol) plus and minus the ninety-five per cent confidence interval (vertical line).

Linear regression analysis of percentage of body water on salinity indicates there was a significant inverse relationship ($n = 190$, $r^2 = 0.03$, $P < 0.05$) between these two variables in males, but no significant relationship existed in females. Analysis of dry weight on temperature does not show a significant relationship for males while a significant positive relationship ($n = 114$, $r^2 = 0.05$, $P < 0.05$) occurred in females.

Male RVM, foot and TDG indexes are found in Figure 1. One way analysis of variance (ANOVA) indicates that all three components showed highly significant variations ($P < 0.01$) with time. However, seasonal changes in the magnitude of the foot indexes were small when compared with changes in the magnitude of the RVM and TDG indexes. There appear to be bimodal patterns present in both the TDG and RVM indexes in 1974. The TDG index reached a primary peak of 2.35 g·100 g animal^{-1} in April, 1974 and a secondary peak of 1.65 g·100 g animal^{-1} in September, 1974. The RVM index peaked at 2.37 g·100 g animal^{-1} in April, 1974 and again at 2.91 g·100 g animal^{-1} in October, 1974. Indexes from April to September dropped to an intermediate value. Indexes in 1973 were generally

higher than those observed in 1974, although sample variation within a month was greater.

Female RVM, foot and ODG indexes are presented in Figure 2. ANOVA indicates that all four components exhibited highly significant variations ($P < 0.01$) with time. However, seasonal changes in the magnitude of the foot and RVM indexes appear to be small when compared with seasonal changes in the magnitude of the ODG and CAG indexes. Seasonal patterns in the ODG are unimodal. This index peaked at 2.30 g·100 g animal^{-1} in April, 1974, declined during the summer months, and eventually reached a low of 0.46 g·100 g animal^{-1} in November. The CAG index peaked at 0.77 g·100 g animal^{-1} in April, 1974. This index dropped to intermediate values in May and June, 1974, showed a slight secondary peak in July at 0.56 g·100 g animal^{-1}, and dropped to a pre–peak low in August, 1974.

Male biochemical level

The mean protein level in males ranged seasonally from 62.07 to 80.24% dry weight in the foot, from 39.34 to 78.14% dry weight in the RVM, and from 23.91 to 61.78% dry weight in the TDG. All three components showed highly significant ($P < 0.01$) fluctuations in protein levels.

Mean carbohydrate level ranged from 6.37 to 11.32% dry weight in the foot, from 7.51 to 17.03% dry weight in the RVM, and from 6.18 to 10.00% dry weight in the TDG. Variations in the RVM and TDG carbohydrate level are highly significant ($P < 0.01$). Male and female monthly variations are discussed further under Duncan's Analysis.

Mean lipid level ranged seasonally from 4.05 to 4.97% dry weight in the foot, from 4.41 to 5.37% dry weight in the RVM and from 11.35 to 18.98% dry weight in the TDG. ANOVA indicates that variations in the RVM and TDG lipid levels are significant ($P < 0.05$).

Female biochemical level

Mean protein level in the females ranged seasonally from 59.63 to 74.58% dry weight in the foot, from 56.39 to 76.59% dry weight in the RVM, from 35.23 to 57.40% dry weight in the ODG and from 41.35 to 80.90% dry weight in the CAG.

Mean carbohydrate level ranged seasonally from 4.95 to 10.25% dry weight in the foot, from 7.79 to 18.85% dry weight in the RVM, from 5.15 to 10.22% dry weight in the ODG and from 4.21 to 14.18% dry weight in the CAG.

Mean lipid level ranged from 3.60 to 4.82% dry weight in the foot, from 4.18 to 5.54% dry weight in the RVM, from 12.26% to 19.55% dry weight in the ODG and from 4.17 to 13.48% dry weight in the CAG. ANOVA indicates that variations in protein, carbohydrate and lipid levels in all four female body components are highly significant ($P < 0.01$).

The highest mean protein level in both males and females was found in the foot and RVM, while the lowest mean level was found in the TDG and ODG. Mean carbohydrate level was generally higher in the RVM of both sexes. Mean lipid level was highest in the gonad digestive gland complexes and lowest in the foot in both sexes.

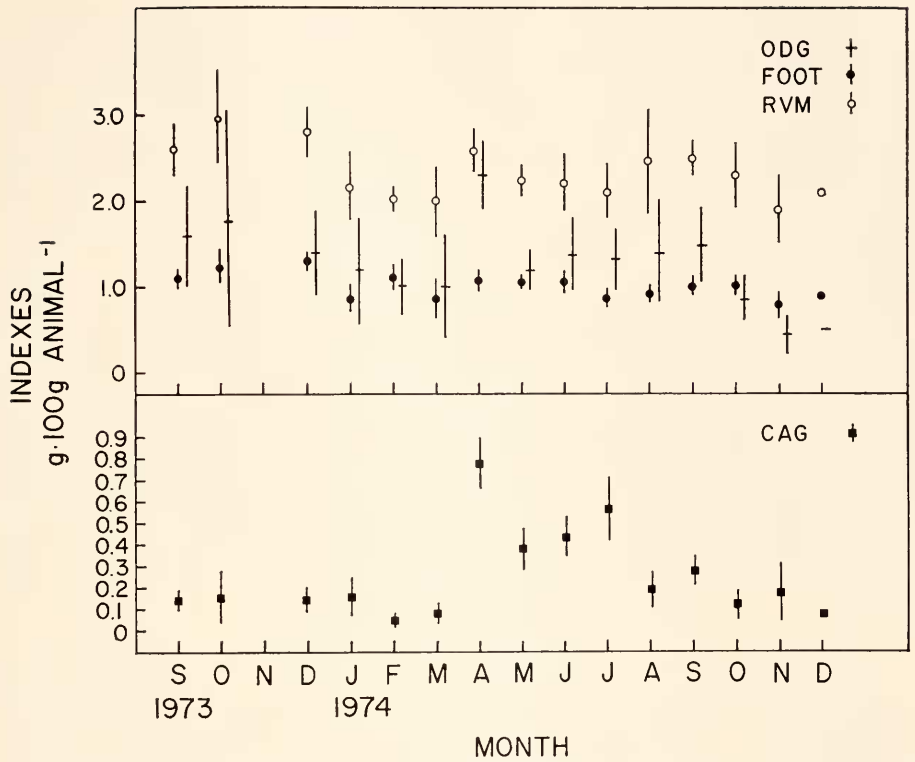

FIGURE 2. Body component indexes in *Thais haemastoma*. Female ovary-digestive gland (ODG), remaining visceral mass (RVM), capsule-albumin gland (CAG) and "foot" indexes are presented as the mean (symbol) plus and minus the ninety-five per cent confidence interval (vertical line).

Male biochemical content

Male protein content ranged from 0.53 to 0.85 g per 100 g animal in the foot and from 1.33 to 2.05 g per 100 g animal in the RVM. TDG protein content was 0.29 g per 100 g animal in February, increased to 1.04 g per 100 g animal in April and leveled gradually to a low of 0.18 g per 100 g animal in December. January TDG and RVM protein content appears to be high when compared with data obtained from other low temperature months of 1974. Variations in protein content in the RVM and TDG are highly significant ($P < 0.01$).

Mean carbohydrate content in the foot fluctuated from 0.06 to 0.13 g per 100 g animal. Mean RVM carbohydrate content increased significantly in April and June over other months. However, RVM carbohydrate content was highest in January with a value of 2.05 g per 100 g animal. TDG carbohydrate increased from 0.08 g per 100 g animal in February to 0.24 g per 100 g animal in April, declining gradually to 0.06 g per 100 g animal in November. ANOVA indicates that variations in RVM and TDG carbohydrate content are highly significant ($P < 0.01$).

Mean lipid content varied seasonally from 0.04 to 0.06 g per 100 g animal in the foot and from 0.10 to 0.15 g per 100 g animal in the RVM. January values for TDG lipid content appear to be abnormally high when compared with mean content values of other months. Mean TDG lipid content values were low in February at 0.17 g per 100 g animal and increased to a high of 0.49 g per 100 g animal in April. Lipid content dropped to 0.16 g per 100 g animal in June and then peaked again at 0.26 g per 100 g animal in September, returning to a low of 0.08 g per 100 g animal by December. ANOVA indicates that variations in mean lipid content in all three body components are highly significant ($P < 0.01$).

Female biochemical content

Mean protein content of females varied seasonally from 0.49 to 0.83 g per 100 g animal in the foot and from 1.15 to 1.77 g per 100 g animal in the RVM. Mean ODG protein content increased from 0.52 g per 100 g animal in March to 1.14 g per 100 g animal in April, dropped to 0.64 g per 100 g animal in May, rose slightly to 0.80 g per 100 g animal in June, and gradually decreased to its lowest value, 0.20 g per 100 g animal, in November. ANOVA indicates that variations in protein content in all three body components are highly significant ($P < 0.01$).

Mean carbohydrate content varied seasonally from 0.05 to 0.11 g per 100 g animal in the foot and from 0.18 to 0.48 g per 100 g animal in the RVM. Mean

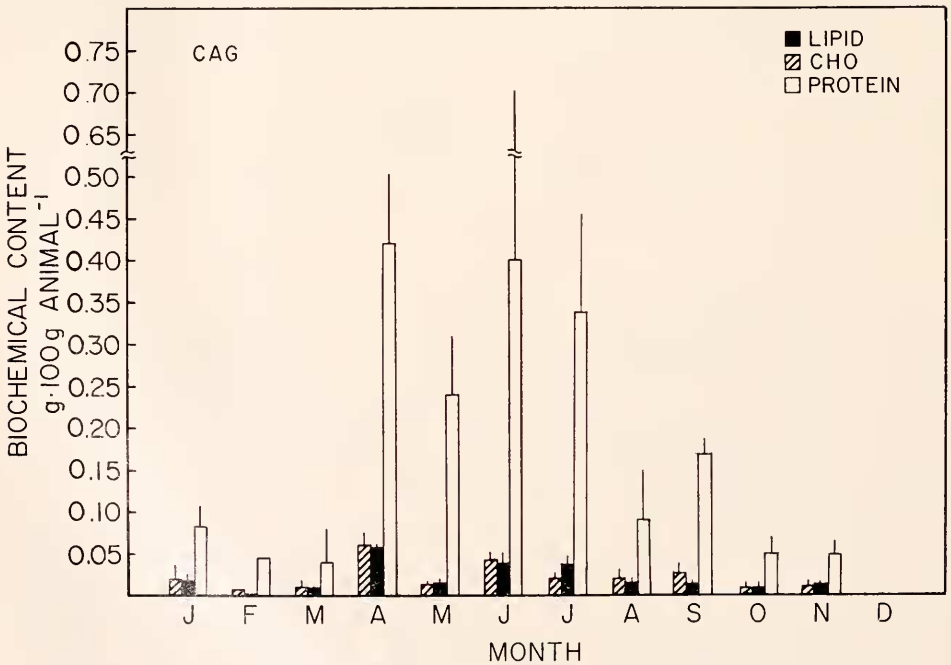

FIGURE 3. Biochemical content in *Thais haemastoma*. Protein, carbohydrate (CHO) and lipid content of the female capsule–albumin gland complex (CAG) expressed as the mean (vertical bar) plus the ninety-five per cent confidence interval (vertical line).

ODG carbohydrate content varied seasonally from 0.03 to 0.22 g per 100 g animal, with the largest increase occurring from 0.09 g per 100 g animal in March to 0.22 g per 100 g animal in April. ANOVA indicates that variations in carbohydrate content in all three body components are highly significant ($P < 0.01$).

Mean lipid content ranged seasonally from 0.04 to 0.05 g per 100 g animal in the foot and from 0.09 to 0.13 g per 100 g animal in the RVM. Mean ODG lipid content increased from 0.15 g per 100 g animal in March to 0.42 g per 100 g animal in April, but dropped to 0.24 g per 100 g animal in May and gradually decreased to a low of 0.07 g per 100 g animal in November. ANOVA indicates that fluctuations in foot and RVM lipid content are significant ($P < 0.05$) while fluctuations in ODG content are highly significant ($P < 0.01$).

Mean protein, carbohydrate and lipid content data in the capsule–albumin gland complex of females are found in Figure 3. All three CAG biochemical constituents showed highly significant fluctuations ($P < 0.01$). Protein content increased from 0.05 g per 100 g animal in March to 0.46 g per 100 g animal in April, but by November had fallen back to 0.05 g per 100 g animal. Carbohydrate content increased from 0.01 g per 100 g animal in March to 0.06 g per 100 g animal in April, and by November had fallen back to 0.01 g per 100 g animal. Mean lipid content increased from 0.01 g per 100 g animal in March to 0.06 g per 100 g animal in April and by November had again returned to 0.01 g per 100 g animal.

Duncan's analysis

Duncan's Multiple Range Test for the variable CAG indicates that this component index cycles in a significant bimodal pattern with peaks in April and July.

Duncan's analysis of male RVM level data indicates that carbohydrate level in this component cycles minimally. Carbohydrate level was highest in January and April and lowest in November. No other components in either males or females exhibited seasonal patterns in biochemical constituent levels.

The male TDG carbohydrate content exhibited a seasonal pattern of cycling. TDG carbohydrate content is significantly higher in April. TDG lipid also cycled significantly; lipid content was highest in April and January, although April was significantly higher than all other months while January was not. Lipid content in October was also significantly higher than November.

Male RVM carbohydrate content was significantly higher in January and April, and male RVM lipid content was significantly higher in April than in all other months.

Duncan's analysis of female biochemical content indicates that ODG protein cycles seasonally; protein content was significantly higher in April, June and January, although June is not statistically different from any other months except October and November. ODG lipid content also exhibited significant seasonal patterns. Lipid content was significantly higher in April than in all other months, while November content was significantly lower than all months except January, May and October.

Female RVM carbohydrate content is significantly higher in April from all months except June, while June is significantly higher than November, but is not different from any other months.

All three CAG biochemical constituents exhibited seasonal patterns of fluctuation. Protein content in April, June and July are not significantly different. April and June are significantly higher than all other months. Carbohydrate content is significantly higher in April than in all other months. June carbohydrate content is significantly lower than April and significantly higher than all other months. Lipid content was significantly higher in April than in all other months. Lipid content in May, June and July were not significantly different from each other but these three months were significantly lower than April and significantly higher than all other months.

Discussion

The major changes observed in both the component indexes and the content of the various biochemical constituents indicate that accumulation of organic reserve material is occurring on a seasonal basis in some body components of *Thais haemastoma*. We found the best component indicator of reproductive readiness in *T. haemastoma* to be the capsule–albumin gland complex. This has also been found true for *T. lamellosa* by Stickle (1973, 1975), *Fusitriton oregonensis* by Stickle and Mrozek (1973) and *Littorina irrorata* by Bistransin (1976). In both sexes copulation and capsule deposition, as indicated by decreases in component indexes, occur after April. The high values for component indexes in May and June suggest that spawning probably occurs intermittently during these months, is intensified after the July sampling data, and continues to occur at a reduced level throughout August. These results need to be substantiated by *in situ* observations of spawning members of the population.

The interpretation of this data is complicated by feeding patterns in *Thais haemastoma*. The secondary peaks observed in both the TDG and ODG may represent preparation for a second period of copulation and capsule deposition or reflect increased feeding and food availability. Peak spatsets of the oyster, *Crassostrea virginica*, occur in May–June and again in September (Pollard, 1973) thus altering food availability to the snails. Recent work by Spight and Emlen (1976) indicates that spawning is influenced greatly by food availability. In *T. emarginata*, for example, spawning rates were found to parallel barnacle densities and spawning frequency was adjusted to the food supply. It is also possible that increases in body component indexes observed in August and September represent storage of reserve material in preparation for the approaching winter months.

Seasonal changes in body component indexes have been observed in other species of *Thais*. Stickle (1973) found unimodal patterns of cycling in the TDG, ODG, and CAG of the west coast *T. lamellosa*, but found no seasonal patterns in the foot or RVM of either sex. The seasonal changes observed in the RVM of male specimens of *T. haemastoma* are difficult to explain. They may be due to cycles in the size of the prostate, the only male accessory organ. The RVM is not generally considered to be a major nutrient storage depot (Stickle, 1973). However, Bistransin (1976) found seasonal changes in the RVM of *Littorina irrorata*. This snail was also found to exhibit a bimodal reproductive pattern with peaks occurring in May and August.

The inverse relationship observed between percentage of body water and ambient salinity in males indicates that body water and total dry weight indexes are in

part a reflection of changes occurring in the total body water in response to fluctuations in salinity. Body water in *Thais haemastoma* has previously been shown to vary between 72.9 and 81.9% during a simulated 30–10–30‰ S semidiurnal cycle, indicating that significant variations are occurring in response to short term fluctuations in ambient salinity (Stickle and Howey, 1975). However, it must be remembered that salinity determinations represent time–point recordings whereas in reality, salinity in the Barataria Bay system fluctuates considerably on both a daily and a seasonal basis (Hewatt, 1955). A temperature–dry weight index relationship was not observed in the male sample. This is probably due to the high index values recorded in the cold months of 1973 as compared with the low indexes recorded in the cold months of 1974. Since index data are not complete in 1973, the significance of the observation is unknown. The direct relationship between temperature and dry weight indexes in the female sample indicates that females mature reproductively at warmer temperatures and is in agreement with increases in the body component indexes observed during the warmer months of 1974.

The lack of a significant relationship between shell indexes and shell weight/shell length ratios indicates that changes in the indexes of the soft body components are due to actual changes in the weight relationship of the soft body parts. Seasonal changes in the shell indexes reflect changes in the sum total of the soft parts and body water and not a cyclical accumulation and mobilization of shell material. Stickle (1973) found similar results in the prosobranch, *Thais lamellosa*.

Changes in the biochemical content of *Thais haemastoma* were found to reflect changes in the respective body component indexes rather than fluctuations in constituent levels. This is not unexpected—most marine invertebrates do not possess distinct storage depots such as those found in the vertebrates (Giese, 1969; Stickle, 1975) and therefore any increases in biochemical substances must represent increases in cellular materials. Protein levels were somewhat higher than those recorded for marine prosobranchs where the Lowry (Lowry, Rosebrough, Farr and Randall, 1951) or Kjeldahl protein nitrogen determination methods were used. Foot protein in *T. haemastoma* comprised 60 to 74% of the entire biomass, while in *T. lamellosa* studied by Stickle (1975) and *Littorina irrorata* by Bistransin (1976) foot protein comprised only 30 to 40%. This may be a result of the differences in techniques used. The Lowry method has recently been shown to produce lower results than the classical biuret analysis when using BSA as a test standard (Bio–Rad Laboratory, Technical Bulletin 1015, 1977). Initial protein determinations on *T. haemastoma* using the Biuret and Lowry methods consistently gave lower values for the same tissue with the Lowry method.

Most of the biomass lost from the female visceral mass (comprised of ODG, CAG and RVM) in *Thais lamellosa* was deposited as capsule material (Stickle, 1973). The CAG produces all of the extraembryonic material surrounding the eggs, accounting for 39 to 45% of the visceral mass lost during aggregation in that species. The CAG in *T. haemastoma* is also the production site of extraembryonic material and the situation in this species is probably very similar to that observed in *T. lamellosa*, accounting for the large changes observed in protein, lipid and carbohydrate in the CAG. Stickle (unpublished data) found the egg capsule composition of *T. haemastoma* to vary with salinity. Capsules deposited at 30‰ S were composed of 53% protein, 7% lipid and 2% carbohydrate. In comparison, capsules

deposited at 17.5‰ S were composed of 36% protein, 17% lipid and 2% carbohydrate. Capsule wall material is primarily protein with a small amount of mucoprotein (Fretter and Graham, 1962) while carbohydrate has been identified in the nutritive fluid of one species of pulmonate (Bayne, 1966). Lipid levels in the CAG are high when compared with the foot and RVM and may represent either a respirative energy source or a nutritive source for the developing embryos. Lipid has been found in the nutritive fluid of *Nucella* (=*Thais*) *lapillus* by Bayne (1968) and Stickle (1975) found lipid levels of 12.9% in the capsules of *T. lamellosa* produced at 30‰ S. Large changes in lipid content in some female components may be masking percent body water–salinity interactions, thus explaining the lack of a significant relationship between these two variables. In the black abalone, *Haliotis cracherodii,* water levels decrease when lipid content in the ovary increases and water content falls considerably just prior to spawning (Giese, 1969).

The ovary and digestive gland are relatively unseparable and it is not clear whether accumulation of biochemical material is occurring in the ovary. It is possible that most increases in reserves occur in the digestive gland, with mobilization and nutrient transfer between the digestive gland and ovary prior to reproduction. Lawrence, Lawrence and Giese (1965) demonstrated an inverse relationship between the digestive gland and ovary in *Katharina tunicata,* suggesting transfer between these two organs. However, studies involving nutrient transfer are limited and much more remains to be done in this area. Nutrient storage in the gonad itself has been shown to occur in oysters and clams (Webber, 1970). Webber (1970) found no cyclical pattern in the digestive gland index of the abalone, *Haliotis cracherodii,* and lipid levels in the gonad were found to correlate with the state of ripeness of eggs.

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Summary

1. Seasonal changes in the body component indexes of *Thais haemastoma* were studied over a 15 month period. Seasonal changes in the protein, carbohydrate and lipid level and content were determined for soft components over a 12 month period.

2. The capsule-albumin gland index was determined to be the best indicator of reproductive readiness in *Thais haemastoma.* This index cycled in a bimodal pattern, peaking in April and July.

3. Male testis–digestive gland and remaining visceral mass indexes cycled seasonally with major peaks in April and secondary peaks in September and

October, respectively. The female ovary–digestive gland cycled in a unimodal pattern, peaking in April. Changes in the shell index of both sexes were found to reflect changes in the sum total of the soft body indexes.

4. Seasonal changes in protein, carbohydrate and lipid content were found to be predominantly due to changes in component indexes and not to fluctuations in constituent levels.

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